THE VELIGER

The Veliger 27(4):386-396 (April 1, 1985)

Shell Growth, Trauma, and Repair as an Indicator of Life History for *Nautilus*

by

JOHN M. ARNOLD

Kewalo Marine Laboratory, Pacific Biomedical Research Center,
University of Hawaii, Honolulu, Hawaii 96813

Abstract. By examining the shells of *Nautilus pompilius,* it has been possible to partially reconstruct the life history of individual animals. Two types of predation were found: (1) boreholes apparently made by an octopod and most frequently occurring over the left retractor muscle and (2) spalls or triangular notches apparently caused by *Nautilus* attacking other *Nautilus.* This intraspecific predation (cannibalism) can be divided into: (1) nips—incomplete penetration of the edges of the shell, (2) bites—removal of beak-sized and shaped pieces of shell, and (3) crunches—removal of large amounts of shell and mantle. Other types of mechanical damage may remove as much as one-quarter of the shell of the living chamber and the animal recovers and secretes new shell with an interruption in shell pattern. Foreign substances in the wound area or damage to the mantle resulted in abnormal shell deposition. Abnormal growth patterns and lumps were frequently observed. Some of these were caused by commensal organisms but others are of unknown etiology. Shell growths were found which appeared to have been caused by tumors of the mantle.

INTRODUCTION

Attempts to study the biology of lesser known animals are frequently frustrated by the very reason for which they are not better known: they are either extremely rare or live in inaccessible places. Although *Nautilus* has great intrinsic interests as the last living remnant of a large and once important marine class (House & Senior, 1981), it remains poorly known because of its remote habitat. Paradoxically, this remote, precise, and stable environment has allowed *Nautilus* to retain its primitive nature. *Nautilus pompilius* is a benthic animal which migrates nocturnally from depths as great as 700 m (Haven, 1972; Saunders & Wehman, 1977) to depths of about 100 to 150 m where it feeds. Even at 100 m, these animals are below the workable range of scuba divers. There are two possible means of study: removal to an artificial environment and use of indirect evidence to gain insight into the life history of *Nautilus.* The latter approach is the subject of this study.

MATERIALS and METHODS

This study was carried out on material collected mainly in October and November 1979 during the last cruise of the R/V *Alpha Helix.* Living specimens of *Nautilus pompilius* were purchased from local fishermen who captured them in split bamboo traps made for the purpose. These traps were set usually at depths of approximately 150 m but each group of fishermen seemed to have favorite depths and locations in the Tañon Strait between the islands of Negros and Cebu (123.2°E, 10°N). Although a variety of different baits was tried, including several varieties of fish, squid, piglets, and puppies, the consensus of the local fishermen was that freshly killed chicken was most effective. Between 12 October and 20 November 1979, 332 adult and juvenile animals were collected and examined and those showing interesting shell abnormalities or damage were reserved for further study. Selection was subjective because of the contingencies of shipboard conditions but tended to be consistent because specific criteria were used. All the animals captured were weighed, sexed if possible, serially numbered, and then held in running seawater (10-15°C) for variable periods of time; then the shells were examined in detail. Some animals were maintained for as long as six weeks in apparent good health.

Shells of living animals that showed repaired damage or other abnormalities were examined to determine if the damage was related to capture and subsequent handling or if it had occurred naturally. Damage associated with recent collection was easy to eliminate because of the newness of the fracture or damage to soft tissues.

Fishermen, shell dealers, and children frequently offered empty *Nautilus pompilius* shells for sale. These shells were also examined for anomalies. Most of these shells were "beach" or "drift" shells which showed evidence of having been dead for some time before collection. Bored shells were included for study. Purchased shells were designated with the prefix "P" followed by a number.

Included in this study are three abnormal shells recently named *Nautilus belauensis* Saunders, 1981, from Palau which were kept in the Waikiki Aquarium for varying lengths of time. They are designated with the prefix "W." The conditions of capture and maintenance are described by CARLSON (1979). The author retains all of these shells for further study.

RESULTS

The types of shell abnormalities that reflect the life history of the individual are categorized as follows: (1) Mechanical alteration of the shell resulting from (a) predatory damage, and (b) repair of mechanical and/or predatory damage. (2) Growth alterations caused by (a) imperfect repair and regrowth, (b) interference by commensal organisms, (c) abnormal and tumorous growth, (d) artificial maintenance, and (e) irregular size change.

Mechanical Alterations

Predatory damage: *Nautilus* shells show two types of damage related to presumed predation: bored holes and bites from the shell. Boreholes in or near the terminal chamber are apparently caused by another mollusk, possibly an octopod. In 1982 I saw a trap set in the Tañon Strait that contained six living *Nautilus pompilius,* one dead *N. pompilius,* and a mature male *Octopus cyanea.* The dead *Nautilus* had a borehole in the shell over the left retractor muscle and a portion of the body had been eaten. The local fishermen who set the trap said this was a common occurrence. These boreholes are ovate to diamond-shaped (Figure 1) and show striations on the side wall. They are subconical in shape and narrowest at the inner peak end. Shape and size are suggestive of the holes produced in *Strombus* and other shells by *Octopus vulgaris* (PILSON & TAYLOR, 1961; ARNOLD & OKERLUND-ARNOLD, 1969; WODINSKY, 1969; NIXON *et al.*, 1980) and in *Nautilus* (TUCKER & MAPES, 1978). Fifteen such boreholes were found in 348 shells (collected and purchased), with one shell having three holes, two having two holes each, and all other shells with one hole each. In 10 of 15 instances, the boreholes were located over the left retractor muscle, and the point of penetration continued through the conchiolin-like layer separating the muscle from the shell and to the muscle tissue itself (Figure 1b).

When the borehole was not over the left retractor, the animal was either given to us live, or reportedly was still alive when taken by the donor. In shell P1, three holes were bored: two were on the right side of the living chamber 8.0 and 8.8 cm from the lip, and the third hole was about 7 mm inside the lower edge of the left retractor muscle. Shell P2 had two completed holes near the midline, one was 6 cm back from the lip and the other was 8.1 cm back and 1.3 cm left of the midline. This animal was in the early stages of forming a new septum. Shell P5 was acquired freshly dead with shreds of drying retractor muscle in place. There was one completed hole 9 cm back from the shell lip 1.2 cm to the right of the midline, and a second hole was over the retractor muscle scar at least 2 cm from the outermost edge.

The second evidence of predation was obtained by direct observation of captive animals. It was frequently noted that one *Nautilus* would grip another so the shell apertures were opposed and the beak of one animal attacked the lip of the shell of the other animal. Pieces of shell could be seen and heard to be broken away in these encounters, which lasted from minutes to several hours (see also WARD & WICKSTEN, 1980). Damage varied in severity and was of three types: nips, bites, and crunches.

Nips are here defined as point breaks through the outer layer of shell (called porcelaneous ostracum by STENZEL [1964]) to the pearly underlying nacreous layer (Figure 2). When freshly produced (*i.e.,* witnessed), these nips are usually within 6 mm of the edge of the shell lip and tend to be oblong and vary in width from 1.2 to 1.5 mm. The bottom of these nips is usually flat. On some occasions the nips penetrate through the shell and are subsequently sealed with a layer of black organic film as described by STENZEL (1964). The nips do not have the characteristic diamond shape and striations of boreholes, and frequently have "shelves" and "plateaus" suggestive of spalls parallel to the surface of the layers. Occasionally several nips coalesce forming a large area of exposed nacre. Occasionally nips could be seen some distance back from the current shell edge indicating subsequent growth had occurred.

Bites are defined as triangular beak-shaped pieces removed from the shell at the edge of the aperture. Bites vary in size depending on how deeply the shell edge was drawn into the jaws. Frequently, they occur in connected linear arrays (Figure 3). On occasion, these arrays extended for several centimeters along the lip of the shell and when combined make deep curved or scalloped indentations (Figure 4) which may be several square centimeters in area (Figure 6). Frequently, cracks that originate at the bite coalesce and remove portions of the shell (see crunches below). Cracks often approximate or parallel the direction of the midline, then suddenly curve off sharply toward one side (Figure 5). This type of break can be easily duplicated by pressure applied to the shell surface with a pair of narrow pliers or, less easily made, by a sharp blow at the lip of a submerged shell. The curved part of the break almost invariably has evenly spaced (harmonic?) chipping along its outer surface. In

12 of 16 shells of females, this excision occurs on the animal's left side.

Crunches are here defined as large areas of missing shell (*i.e.,* several times larger than the beak area). These may result either from the coalescence of several bites into a common break or from the intersection of cracks. Possibly some of these large "crunches" are the result of mechanical damage caused by accidental contact with hard surfaces or even by attacks by larger unknown animals (*e.g.,* possibly by turtles, LEHMANN, 1981), but because of the association of the easily identifiable bites near the crunches, it appears that at least some are caused by fractures related to the bites (Figure 6). The mechanical damage and large areas of damage resulting from bites or other unknown factors will be considered together for purposes of discussion.

Repair of mechanical and/or predatory damage: Almost every shell examined in this study showed some evidence of repaired predation or other damage. The degree of repair and retention of the original shell proportions varied with the extent of shell and underlying mantle tissue damage. If the mantle was extensively damaged (*e.g.*, by attack from another *Nautilus*), the shell was frequently imperfectly repaired and subsequent outgrowth was abnormal. The effect on the shell varied from interruption of the striped color pattern to discoloration of the junction of new and old shell to extensive rough-ribbed irregular areas covered with layer(s) of black organic material (Figure 7). The damaged mantle sometimes apparently gradually recovered during regrowth and the distal shell again became smooth (Figures 5, 8). However, in other cases the damaged mantle continued to lay down abnormal shell, and the width of the longitudinal stripes enlarged in proportion to the expansion of the shell diameter (Figure 7). It was not possible to derive an exact estimate of the percentage of shells with repaired breaks because early damage is covered by subsequent whorls and some later damage is repaired, but of the 332 shells examined in the 1979 collection only a few animals (less than 2%) were judged to be unflawed by breakage at some time in their life span. Because of shipboard limitations, it was not possible to determine experimentally how much of the shell could be removed without causing death of the animal but, judging from repaired natural breaks (*e.g.*, Figure 9), at least one-quarter of the shell could be missing and eventually replaced. There was no way of estimating the amount of soft tissue that could be lost, but Figure 10 shows an

→

Explanation of Figures 1 to 12

Figure 1a, b. a. Position of the borehole over the left retractor muscle. Note also that this shell had serpulid tubes near the lip and the barnacle basal plate near the umbilicus (*cf.* Figure 24). b. Higher magnification of the borehole shows it to resemble strongly those found drilled in *Strombus* shells by *Octopus vulgaris.*

Figure 2. "Nips" at the edge of the shell. These are shallow depressions which occasionally penetrate the shell. Penetrations become plugged with a layer of black organic material (broad arrow) (shell 363).

Figure 3a, b. a. "Bites" witnessed being taken by aquarium specimens in the shell of *Nautilus.* b. Bites on the edge of the shell of a collected specimen. These bites are the size and shape of the adult beak. There is also a repaired "crunch" on the left of the midline (arrow) (shell 441).

Figure 4. Damage from repeated bites on the shell. This animal has obviously been attacked frequently and the mantle was damaged at the midline so that it secreted abnormal ribbed shell. The mantle damage on the left side eventually was overcome and normal shell was again produced (shell 489).

Figure 5. Break and loss of shell probably due to joined cracks resulting either from a bite or from mechanical damage to the shell. The curved portion of the break has harmonic chipping all along the edge. Note the abnormal shell outgrowth (arrow) which resulted from mantle damage. This suggests the break may have originated from cracks due to bites.

Figure 6. Crunches are caused either by environmental damage or by coalescence of several bites into a common large break. There is a tendency for these crunches to be on the left side of the females which is where the beak of the male would make easiest contact during copulation. The arrows indicate abnormal shell outgrowth probably caused by mantle damage that eventually regenerated (shell 576).

Figure 7. Abnormal outgrowth after damage to the mantle. Black organic material is laid down upon normal shell and the shell is deeply ridged. This black material may be subsequently lost resulting in longitudinal striations of the shell (shell 449).

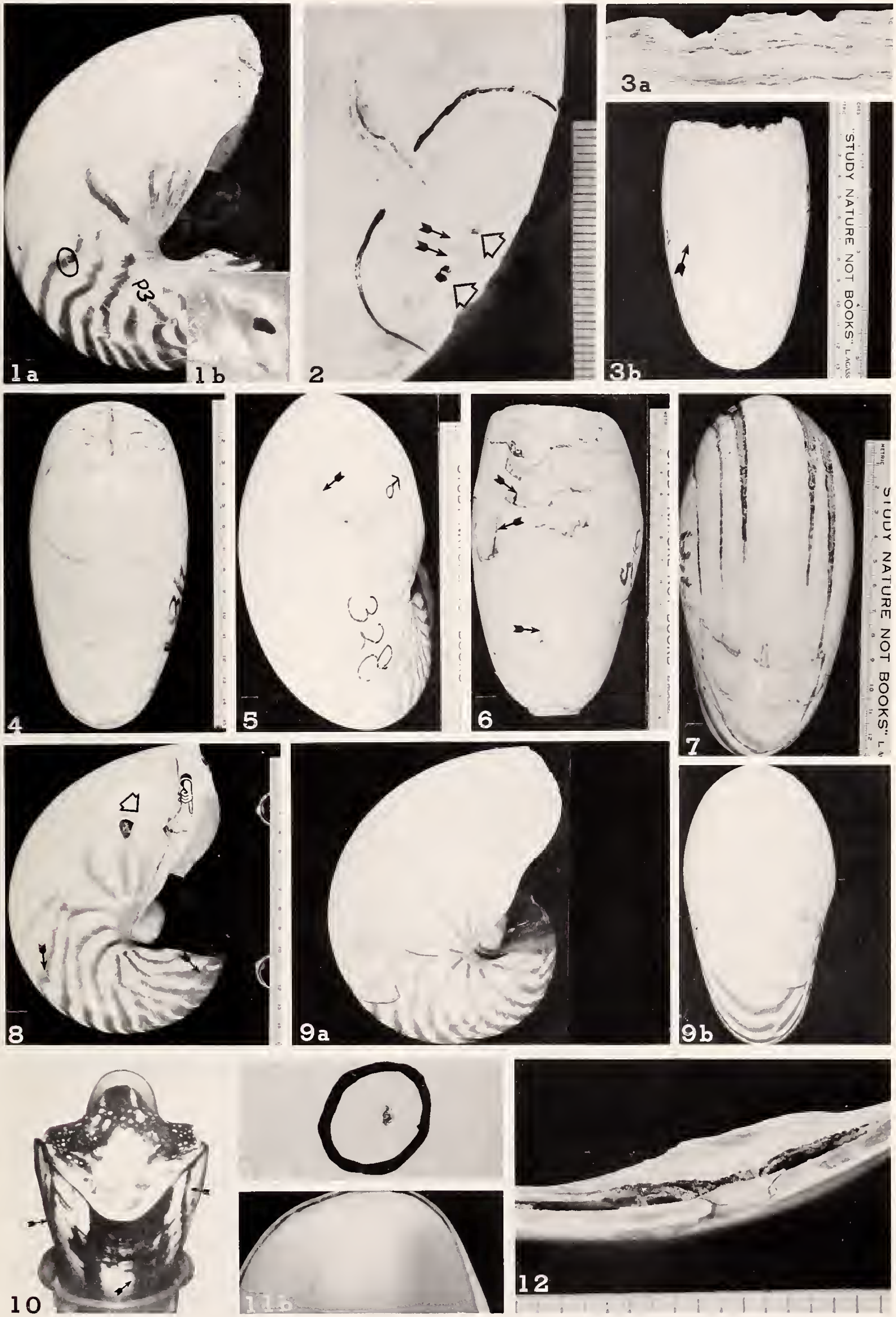
Figure 8. Abnormal outgrowth and repair of the shell as well as recovery of the mantle tissue (narrow arrow). At the broad arrow a large area of shell was cracked and elevated. The mantle then laid down an internal patch that was connected to the old outer shell by black organic material and small spheres of shell. Subsequent repair to damage along the black line resulted in a single layer of shell being formed. Note the bites evident at the black line and the recovery of mantle damage (pointer) near the lip (shell P11).

Figure 9a, b. An extensive area of shell was replaced and the stripe pattern was not resumed in the new shell (shell 182).

Figure 10. About one-quarter of the hood has been bitten off on this specimen and extensive damage to the shell was evident (arrows). Several severed arms and the buccal mass are evident and are apparently in active regeneration (shell 357).

Figure 11a, b. Patched area of shell penetration. In "a" the circle approximates the area of the internal patch. In "b" the patch can be seen to be composed of several layers of shell (shell 332).

Figure 12. Section of the patched region of shell 332. A space exists between the old damaged shell and the newly laid patch. Black organic material covers the inside of the patch.


1a
1b
P3
2
3a
3b
"STUDY NATURE NOT BOOKS" L.AGASS
4
5
6
7
"STUDY NATURE NOT BOOKS" L.A
8
9a
9b
10
11b
12

animal in which extensive damage to the cirri, hood, buccal mass, and shell has occurred (probably due to attack by another *Nautilus*) and regeneration was occurring.

Growth Alterations

Imperfect repair and regrowth: Completeness of damage repair was proportional to the severity of damage. Where the shell was not completely penetrated by a nip, there was usually no repair, or at most a thin layer of non-reflective white material was laid down inside the shell. Where the shell had been penetrated, a pearly material was laid down upon the organic black material. Figures 11a and b show the outside and inside of a shell apparently partially penetrated by a sharp object (perhaps the lower jaw of the beak). The shell at the exact point of impact was partially crushed and fragments remained in the area. The mantle laid down several concentric layers of shell inside the point of penetration, building up a total thickness of 2.56 mm as compared with a thickness of 1.05 mm in the unaffected area (Figure 12). In shell 312 (Figure 13), there were two points of penetration that forced pieces of shell inward. These crushed pieces were subsequently covered by a layer of black organic material and an irregular pearly layer was built up on it that completely closed both openings (Figure 13b). In its thickest area, the pearly material was 2.12 mm thick, not including the organic layer. No new shell was cemented directly upon the damaged shell, rather it was laid down upon the black organic material.

In some cases where the shell was penetrated, foreign material accumulated between the shell and the mantle tissue that apparently altered shell deposition. In shell 438 (Figure 14) the outside of the shell was penetrated and a tunnel continued internal to the damaged area. When the animal had been freshly removed from the shell, the hole had a characteristic rank odor. This odor has been noticed in other animals with abnormal shells. There was no trace of any burrowing organism visible with a dissecting microscope before or after the shell was sectioned. The damage was apparently repaired before the proximal hole was formed, as the removed distal shell had been replaced to a thickness of approximately 1 mm. The inside of the proximal hole had an ovate opening 1.16 cm long which was surrounded by a thickened area about 4.6 mm in maximal thickness and covering approximately 37 cm^2. The inside and outside openings were connected by an irregularly angled opening. In section the thickened area can be seen to be made of several layers of laminar shell laid down upon sheets of black organic material and interspersed with granular, gray, amorphous, loose material (Figure 14c).

In three other instances, abnormal growths were observed in shells in the 1979 *Alpha Helix* collection. In shell P15 (Figure 15) an abnormality of unknown origin caused growth to cease at the midline. Eventually growth was retarded along the leading edge and a line of black organic material accumulated. The source of the outside line apparently was correlated with an internal abnormality within the shell itself that ended at the beginning of the external deformation. A line of irregular black organic material was found within the nacreous layer and porce-

⟶

Explanation of Figures 13 to 19

Figure 13a, b. Repair of a double penetration. There is a layer of black organic material between the old shell and the newly deposited pearly layer.

Figure 14a, b, c. Traumatic shell growth caused by an open hole into the space between the mantle and shell. There are several layers of black organic material alternating with irregular small spheres of shell and organic debris. The inner surface of the repaired shell is non-reflective and porous, and gray in color. No prismatic or columnar shell is evident and a pearly layer is absent (shell 438).

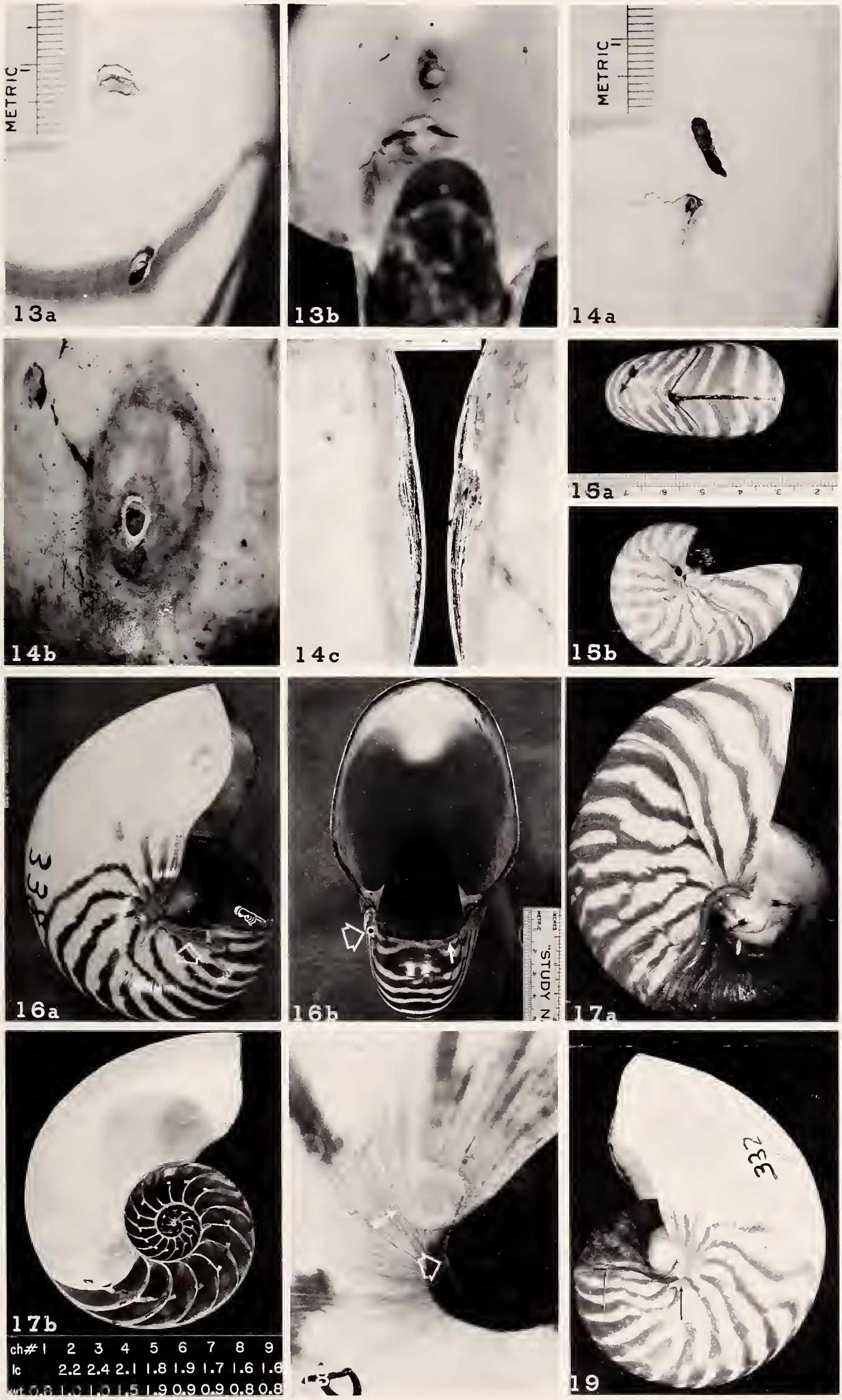
Figure 15a, b. Cessation of growth by internal shell abnormality. The arrow indicates the approximate beginning of an internal linear area of black organic material similar in appearance to the external black line. Growth ceased for a time when the abnormal shell reached the outer shell surface and a line of black material was laid down at the then distorted edge of the shell (shell P15).

Figure 16a, b. A large serpulid worm (broad arrow) in the umbilical region has inhibited outgrowth of the hood and a layer of pearly shell about 1 mm thick has been laid down (pointer). The original margin of the black organic material in the umbilical region has been retracted about 0.5 cm (arrows).

Figure 17a, b. Inhibition of growth by two serpulid worms in shell 337. In this case two small serpulid worms developed in the umbilical region (arrows indicate the ends of the worm tube). Apparently when the *Nautilus* tissues encountered the worm tubes, growth was inhibited until the worm tubes were completely covered with black organic material and some shell because a strong black line delimits the former lip and the pattern of striping is interrupted (a). This shell was sectioned (b) and it was apparent that the uniform increase in chamber size was interrupted (lc = length of the chamber in cm at the outside midline) and during this time the shell increased in thickness (wt = wall thickness at the outside midline in mm). Normal chamber size increased again and the shell regained its normal thickness; apparently then the obstructing worm tubes had been covered. For purposes of presentation the chambers are numbered in reverse order of appearance.

Figure 18. Barnacle basal plates in the umbilical region. A secondary limit of the black organic layer was developed about 3.3 mm back from the original margin (broad arrow).

Figure 19. Shell 332 with putative growth inhibition caused by coralline algae in the umbilical region (arrows).


13a
13b
14a
14b
14c
15a
15b
16a
16b
17a
17b
19
METRIC
METRIC
"STUDY N
338
332
ch# 1 2 3 4 5 6 7 8 9
lc 2.2 2.4 2.1 1.8 1.9 1.7 1.6 1.6
wt 0.8 1.0 1.0 1.5 1.9 0.9 0.9 0.8 0.8

laneous ostracum. This line began as a few black specks 1.7 cm proximal to the former shell lip, and it expanded laterally and vertically producing an elongate irregular space filled with unoriented layers of black organic material. At maximum it was 3.05 mm wide but less than 0.5 mm thick. No identifiable remnant of any substance of animal origin was found. The shell resumed growth after a period of inhibition and the color pattern was reestablished. At the inner margin of the umbilicus a space 2.5 × 2.0 mm caused by centrifugal displacement of the distal-most chambers curved backward at least several mm (Figure 15b). Growth in volume of the chambers from the first chamber to the seventh was uniform, decreased sharply (probably due to hatching, COCHRAN *et al.*, 1981), then resumed increasing uniformly again until the thirteenth chamber which measures 6.7 mm at the outer midline as compared with 7.8 mm for the twelfth chamber and 8.0 mm for the fourteenth chamber. From the fourteenth chamber outward, the chambers increase uniformly.

Interference by commensal organisms: Many specimens of *Nautilus pompilius* had commensal organisms growing on them. Ectoprocts commonly were found in a midline patch extending from a few centimeters beyond the edge of the dorsal mantle fold to the point at which the stripe pattern ends. The ectoprocts apparently did not damage the shells. Depending on position and size, serpulid worms and at least two species of coralline algae did interfere with growth (Figures 21, 22, 23, 24). Large serpulid worms in the umbilical area seemed to cause the most shell response (shell 338, Figure 16). At first the tube was oriented radially toward the umbilicus; then, perhaps on contact with the hood, it deviated and followed the contour of the hood. At the posterior edge of the hood, a layer of pearly shell approximately 1 mm thick and 1 cm wide was laid down upon the black organic film. Total growth was apparently retarded because the original leading edge of the black material was retracted about 0.5 cm on the umbilical region opposite the worm tube. Shell 337 shows stronger growth inhibition evidently caused by serpulid worms (Figure 17). Two worm tubes were laid down in each umbilical region when the shell was several chambers smaller than when captured. They were eventually covered with black organic material and reduced to a low ridge. The worm tubes, however, (1) inhibited growth and a black line developed at the edge of the immature lip, (2) interrupted uniform chamber growth, and (3) changed the thickness of the shell (Figure 17b). Apparently when the worm tubes were encountered, chamber growth suddenly decreased and the outer shell wall increased in thickness from less than 1 mm to 1.9 mm for the next chamber, then decreased to 1.5 mm thick in the following chamber, then resumed a thickness of 1 mm again in the next chamber. The position of the black line coincides exactly with the position of the lip at the time of worm tube interference (Figure 17a).

Growth was seemingly inhibited by barnacles at the edge of the right umbilical region of shell P3 (Figure 18). There is a secondary layer of black film 3.3 mm back from the edge of the maximum extent of the underlying black film. On shell 332 a pink coralline alga has encrust-

→

Explanation of Figures 20 to 26

Figure 20a, b, c, d. Effects of a massive shell inclusion of unknown etiology upon subsequent growth of the whole animal. a. Shows there was a sharp break in the uniform volume increase (arrow) of the shell. The shell was thickened on this side. b. Shell sectioned to show the inclusion *in situ* (shell slightly tipped to facilitate visibility). The proximal portion is covered with a layer of shiny shell. c. Higher magnification of the inclusion. Three areas are evident: the hard shiny proximal area (1) is separated from a layered gray area (2) by an area of mixed black organic material and irregular spheres (3). d. Section through the inclusion showing a layer of prismatic shell (ps) proximally covering an area primarily filled with layers of black organic material upon which spherical gray shell has been laid down (bmss) followed by thin stacks of layers of whitish shell (shell 506).

Figure 21. Solid pearly inclusion in shell 303. When this lump was sectioned, it was found to be pure pearl, and no obvious irritant or growth inducing substance was evident.

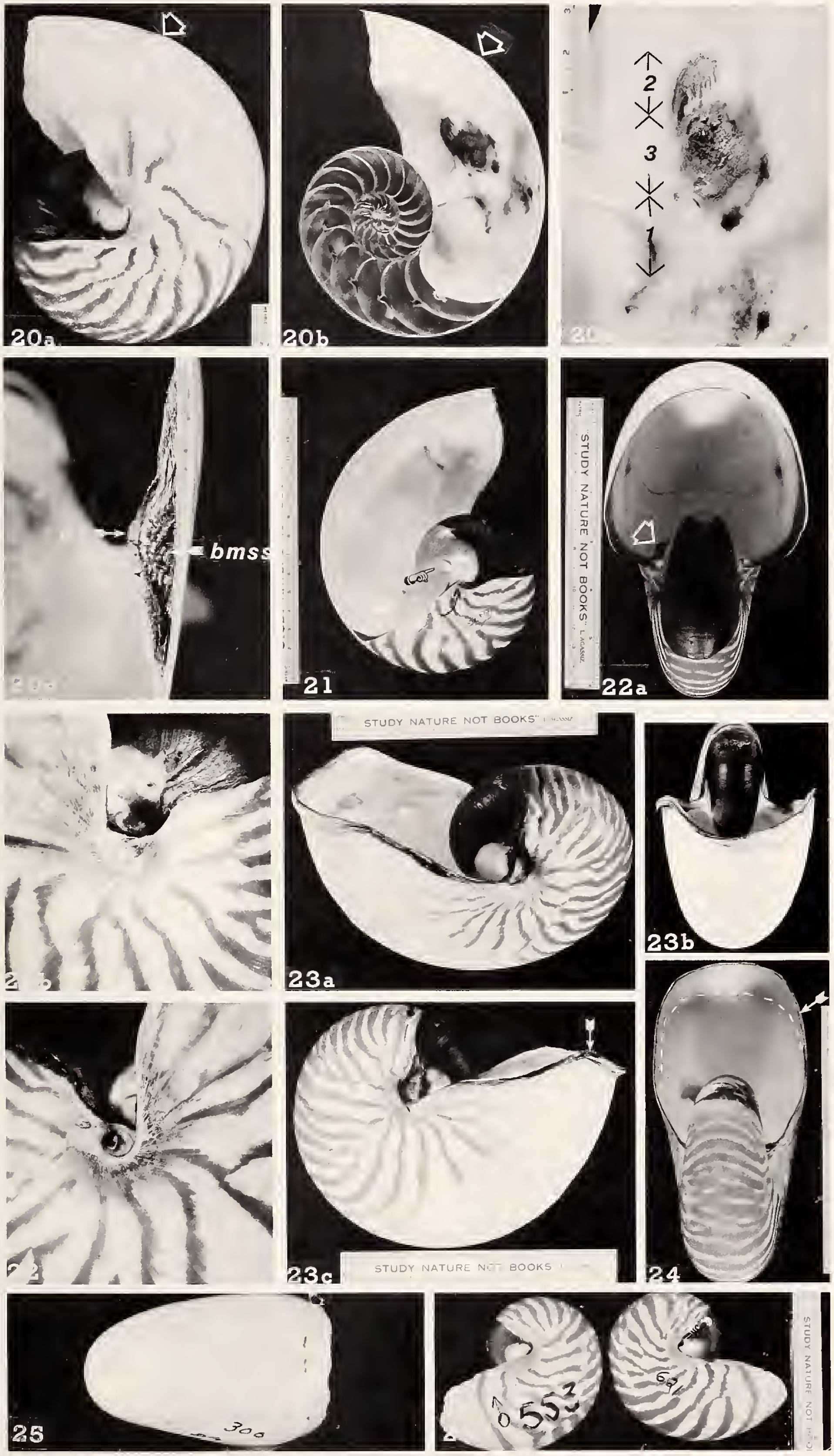
Figure 22a, b, c. Shell W8 (*Nautilus belauensis*) has an open umbilicus on the right side of the shell (Figure 22c) and on the left side the umbilicus is closed (Figure 22b). Inside the left umbilicus there is a large inclusion which may possibly have interfered with shell secretion in this area (Figure 22a).

Figure 23a, b, c. Shell W9 (*Nautilus belauensis*) was kept in the Waikiki Aquarium for about 14 months during which time the shell grew abnormally outward from the lip. Note the secondary line of black organic material across the umbilicus (a, b) and the alternation of the layers of black organic material and shell (arrows).

Figure 24. The edge of shell W6 (*Nautilus belauensis*) had extra pearl laid down upon the inside of the lip. The dotted line indicated the approximate limit of the new pearly layer. The arrow indicated alternation of black organic material and white shell.

Figure 25. Shell 300 shows an abrupt decrease in the size of the living chamber for unknown reasons. It appears the relatively slight damage at the midline and right side occurred after the shell diameter had begun to decrease. There is a line of black organic material at the margin where the decrease began. This was an immature female.

Figure 26. Comparison of two juveniles taken from the same locality in the Tañon Strait. The right shell has an open umbilicus.


20a
20b
2
3
1
bmss
21
STUDY NATURE NOT BOOKS
22a
STUDY NATURE NOT BOOKS
23a
23b
23c
STUDY NATURE NOT BOOKS
24
25
300
0553
STUDY NATURE NOT

ed the umbilical area (Figure 19) and the nearby shell aperture. This animal appeared to be mature judging from a line of black organic material at the lip overlain by thin pearl. The posterior margin of the hood had retracted about 4.5 mm from the edge to a new layer of pearl about 1 mm thick laid upon the black film. A small empty worm tube 1.22 cm behind the leading edge of the lower aperture apparently did not inhibit growth.

Abnormal and tumorous growths: In shell 506 (Figure 20) an abnormal growth of unknown cause inside the shell affected subsequent growth of the animal. The outer third of the living chamber is decreased in size (arrow) and a dark line runs from the left umbilical region to 2.2 cm to the right of the midline. The right side of the living chamber decreases in diameter by several millimeters and the shell is thickened in the incurving region. A few bites taken near the midline and edge appear to have occurred after the chamber volume decrease. The abnormal growth extends from a thick region 12 cm back of the shell lip to about 5 cm from the lip. Distally it is covered with a thin but regular layer of pearly shell enclosing a lump 0.918 cm thick at its maximum. This layer grades into prismatic blocks that eventually grade into a thin gray layer upon a multilayered area that eventually fuses to the shell of the chamber (Figure 20d). Inside this abnormal growth the distal thickened portion is composed of thin sheets of shiny black organic material alternating with spaces crowded with spherical lusterless gray droplets. These droplets average less than 0.5 mm in diameter and tend to occur in stacks, or where exposed to the surface they form loose discontinuous sheets. Toward the mantle, the layers of gray droplets intergrade into prisms of white shell material packed together in rhombohedric columns. The prisms frequently have horizontal sheets of black organic material intersecting them. Approximately the distal 2 cm of this abnormal growth is arranged into sheets of calcareous material laid down upon the layers of black organic material which are spaced an average 0.2 mm apart. These sheets open outward so the areas between them communicate with the mantle space. The whole abnormal growth lies upon a layer of shell secreted upon the original shell (Figure 20d). There are two distinct ridges of hard thickened shell covered with clear chonchiolin which run from the edges of the growth to the columella and underlie the retractor muscles. No external wound appears associated with this internal growth which arises proximally without any evident source and tapers distally to normal appearing shell. Laterally it joins the surrounding shell with areas of brownish-black discoloration. There was no striking gross difference in the mantle when this animal was removed from its shell. In shell 303 (Figure 21), a solid lump 7.5 × 4.5 × 3.5 mm projected toward the body from the inner side of the whorl opposite the attachment of the retractor muscle. When this lump was sectioned, it was found to be pure pearly shell with a homogeneous structure. There was no indication of any irritant or substance that would have induced this growth.

Artificial maintenance: Shells of three animals recently described as *Nautilus belauensis* (SAUNDERS, 1981) were kept in the Waikiki Aquarium for various lengths of time and all showed abnormal growth. The right side of shell W8 has an open umbilicus that extends at least 2.7 cm inward (Figure 22). It is not filled with the hard callus typically found in *N. pompilius* from the Tañon Strait. The left umbilicus is covered with a layer of shell leaving a shallow depression. Immediately inside the aperture near the left umbilicus, there is an incrustation composed of black organic material, pearly shell, and dense discolored shell that projects about 7.2 mm into the living chamber. It is about 1.76 cm wide and about 1.6 cm in length. It has an irregular conical shape with an outwardly directed opening. The black organic layer on the inner whorl was asymmetrical on this animal.

Shell W9 (Figure 23) was kept in captivity for about fourteen months (CARLSON, 1979), during which time growth was asymmetrical and the shell was atypically thickened with a heavy pearly layer averaging 2.6 cm wide. In places the new shell was slightly thicker than 4.1 mm but averaged 3.5 mm thick for most of its extent. This pearl appeared to be laid down upon a thickened edge of several layers of black organic material. On the right side, the shell lip is recurved upon itself and has an irregular contour. The umbilical region has a secondary thickened layer (about 1.5 mm) of black organic material laid down on the original thin layer but back from the margin about 1.2 cm. A third specimen of *Nautilus belauensis* (W6) kept in the Waikiki Aquarium has a completely open umbilicus and also shows a layer of shiny pearl that has seemingly thickened the lip for a width of about 2.35 cm. This shell also has several irregular layers of black organic material interspersed between the shell layers at the extreme edge (Figure 24).

Irregular size changes: Occasionally there are shells that seemingly exhibit uniform shell growth until, for unknown reasons, the diameter of the outer chamber abruptly decreases in diameter (Figure 25). Sometimes these growth decreases seem to correlate with obvious shell trauma (breakage or internal growths) (Figure 16), but often the cause is not obvious. In two cases juvenile *N. pompilius* caught in the Tañon Strait did not have the umbilical region covered by shell and thereby superficially resembled *Nautilus macromphalus* (Figure 26). There was no detectable growth inside the shell similar to that in shell W8 reported above.

DISCUSSION

From the above results, it is evident that a partial history of the life of an individual *Nautilus* is laid down as the shell is secreted, repaired, or added to during the life span.

With reasonable care, it is possible to interpret this record and thereby indirectly gain insight into the environmental and, to some extent, physiological stresses encountered by *Nautilus*. The following life history events are discussed: (1) evidence of predation by known predators, (2) repair of shell damage, (3) imperfect growth and/or regrowth, (4) influence of commensal organisms, (5) anomalies of shell deposition (tumors), (6) environmental inadequacies of artificial maintenance, and (7) size changes due to unknown causes.

Predation: Two of the many possible types of predators have been tentatively identified: *Octopus* and *Nautilus*. The boreholes found in *Nautilus* shells resemble the holes bored by *Octopus* in other molluscan shells (Pilson & Taylor, 1961; Arnold & Okerlund-Arnold, 1969; Wodinsky, 1969; Nixon, 1979a, b, 1980). The size, shape, and texture are similar. The rasp marks, however, may be a product more of the type of shell being drilled than a characteristic of the predator (Nixon, 1980). It is hard to imagine any animal other than *Octopus* being responsible because of the requirement of swimming by the predator and the ability of the predator to learn to position the borehole exactly over the retractor muscle (*cf.* Arnold & Okerlund-Arnold, 1969). Furthermore, the presence of an *Octopus cyanea* in the same trap as a bored and partially eaten *Nautilus* is strong circumstantial evidence that *Octopus* is a predator upon *Nautilus*. In drilling *Strombus* shells, *Octopus vulgaris* consistently drills in a particular location (Arnold & Okerlund-Arnold, 1969; Wodinsky, 1969). In *Nautilus,* holes bored in places other than over the retractor muscle were apparently unsuccessful. Living *Nautilus* specimens were captured with complete boreholes *not* over the muscle but shells that contained living animals were never found with completed boreholes over the muscle area. The tendency to drill on the animal's left side may possibly be due to the right-hand position of the beak of the male which would make an attacker to the right side more vulnerable to counterattack. Therefore, there would be an advantage to learn to bore consistently over the left retractor muscle.

That *Nautilus* is preyed upon by other *Nautilus* was directly established. Almost all shells show evidence of beak-shaped bites and attacks of this type were witnessed. Frequently during copulation the male bites the shell, mantle, hood, and arms of the female in his grasp. Because of the off-center position of the spadex, the male's beak opposes the left side of the female's midline, and there is a tendency (12 of 16 cases) for the females to have more repaired crunches on the left side. The question remains whether the encounters are lethal; in the case of the animal shown in Figure 10, extensive damage was done yet regeneration was occurring. If not lethal, attacks must be detrimental because repair and regeneration require metabolic effort.

Repair of shell damage: The most striking damage involved the breaking away of large areas of shell (Figures 5, 6, 9). It is not possible to identify the causes of all the large breaks but certainly some must be the result of conjoined cracks from bites. Displaced edges are frequently rejoined by a layer of black organic material which later becomes covered by shell (Figure 8). In other cases a line of new shell secretion starts proximal (posterior) to the fissure giving the impression that the mantle retracted and then began to move outward again as it secreted replacement shell. Thus, extensive areas of original shell lined with new shell are common. At the junction of the "new" and "old" shell, there may or may not be a layer of black organic material underlying the new shell.

Imperfect growth and/or regrowth: The success of regrowth of shell (replacement as opposed to repair of damaged but still present shell) seems dependent on the extent and severity of the original damage. If the mantle was damaged, subsequent secretion of new shell frequently was abnormal (Figures 7, 8, 10). Apparently the interjection of foreign substances into the wound area resulted in abnormal regrowth (Figure 14). In most instances the mantle responded to shell trauma by first covering the damaged area with black organic material which was, in turn, covered with shell. In these cases the shell apparently was of uniform density and structure unlike the abnormal (tumorous) shell seen in Figures 14 and 20.

Influence of commensal organisms: Apparently, anything that physically inhibits advance of the body will interrupt the advance of the body whorl. Objects such as worm tubes, barnacles, or even such flat encrustations as coralline algae will interrupt growth. Landman (1983) also observed that barnacles would inhibit *Nautilus* shell growth. This interruption of growth results in thickening of the shell and the interruption of uniform volume increases of the chambers (Figure 17). The thickening of the shell wall suggests that despite interruptions of outgrowth of the living tissue, secretion of the shell continues at a uniform rate. Further growth apparently is dependent upon the ability of the mantle and soft tissues to overcome or cover the interfering foreign objects with hard tissue. In most instances a layer of black organic material is laid over the foreign object. Apparently, when chamber outgrowth is inhibited by a foreign object in the umbilical area, the mantle retracts slightly and begins to secrete pearl over the black layer. Once the obstruction is overgrown or in some way removed, growth resumes, leaving a record as a decrease in chamber size, thickening of the shell, a layer of black material, or a combination of these demarcations.

Anomalies of shell deposition (tumors): Examination of the growths deposited in the shell shown in Figure 20 and similar shells shows that the three normally coordinated steps of shell secretion can become disassociated. Instead of a uniform laying down of shell components upon and among the organic matrix, the black organic material is laid down in macroscopic sheets interspersed with either prismatic masses of shell or aggregates of granular material. Obviously, this reflects the pathological state of the secreting mantle and fits the definition of tumorous growths. Unfortunately, the mantles that secreted these growths are not available for histological examination.

Environmental inadequacies of artificial maintenance: Figures 23 and 24 illustrate two shells of animals that were held in captivity and abnormal growth occurred at the shell lip of these presumably mature animals. MARTIN *et al.* (1978) have figured similar abnormal growth in a specimen of *Nautilus macromphalus* kept in captivity. Because the animals shown in Figures 19 and 20 were kept at typical environmental temperatures, it can be assumed that temperature is not the sole factor in this abnormal growth. Possibly either the conditions of maintenance were inadequate (in the same way in New Caledonia and Hawaii, which seems unlikely) or (more likely) irritation to the shell lip and mantle caused by continued contact with the walls of the container caused abnormal growth.

Size changes due to unknown causes: The cause(s) of the decrease in diameter of the terminal chamber in some shells is an open question without the soft parts. Whether this was from the need to regenerate lost tissue, as would be the case of the animal of Figure 10, or from disease or other metabolic upset requires further study.

CONCLUSIONS

It seems possible to infer by indirect methods that *Nautilus* living in their natural deep sea environments are: (1) subjected to predation by a hole-boring animal, probably an octopod, and certainly by other *Nautilus*; (2) damaged by massive mechanical shell breakage which they are able to repair and compensate for; (3) inhibited in their growth by the presence of external commensal organisms and possibly unfavorable or physiological conditions; and (4) subject to abnormal shell growth caused either by environmental conditions or tumorlike pathologies of unknown etiology. These changes in shell morphology should also be an event in the fossil record.

ACKNOWLEDGMENTS

I would like to thank Dr. Dale Bonar for reading and improving this manuscript, Ms. Lois D. Williams-Arnold for her help in the early phases of this work, Mrs. Frances Okimoto for preparing the manuscript, Miss Andrea Novicki for her photographic expertise, and Mr. Wilson Vialoces for providing the animals used in the study. The staff of the Waikiki Aquarium, particularly Mr. Bruce Carlson, provided the artificially maintained animals. The Republic of the Philippines graciously allowed the R/V *Alpha Helix* to carry out its mission in their national waters, and the National Science Foundation of the United States provided financial support (Grant #PCM 77-16269). Finally, I would like to thank the crew of the *Alpha Helix* and my many scientific colleagues who made this work possible, and the staff at Scripps Institute of Oceanography who supported this cruise.

LITERATURE CITED

ARNOLD, J. M. & K. E. OKERLUND-ARNOLD. 1969. Some aspects of hole-boring predation by *Octopus vulgaris*. Amer. Zool. 9:991–996.

CARLSON, B. 1979. Chambered *Nautilus*: a new challenge for aquarists. Freshwater Mar. Aquar. 2:48–51.

COCHRAN, J. K., D. M. RYE & N. H. LANDMAN. 1981. Growth rate and habitat of *Nautilus pompilius* inferred from radioactive and stable isotope studies. Paleobiology 7:469–480.

HAVEN, N. 1972. The ecology and behavior of *Nautilus pompilius* in the Philippines. Veliger 15:75–80.

HOUSE, M. R. & J. R. SENIOR. 1981. The Ammonoidea: the evolution, classification, mode of life and geological usefulness of a major fossil group. Academic Press: London.

LANDMAN, N. H. 1983. Barnacle attachment on live *Nautilus*: implications for *Nautilus* growth rate. Veliger 26:124–127.

LEHMANN, U. 1981. The ammonites. Cambridge University Press: London.

MARTIN, A. W., I. CATALA-STUCKI & P. D. WARD. 1978. The growth rate and reproductive behavior of *Nautilus macromphalus*. N. Jb. Geol. Palaont. Abh. 156:207–225.

NIXON, M. 1979a. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. Malacologia 18:431–443.

NIXON, M. 1979b. Has *Octopus vulgaris* a second radula? J. Zool. (Lond.) 187:291–296.

NIXON, M. 1980. The salivary papilla of *Octopus* as an accessory radula for drilling shells. J. Zool. (Lond.) 190:53–57.

NIXON, M., E. MACCONNOCHIE, & P. G. T. HOWELL. 1980. The effects on shells of drilling by *Octopus*. J. Zool. (Lond.) 191:75–88.

PILSON, M. E. Q. & P. B. TAYLOR. 1961. Hole drilling by *Octopus*. Science 134:1399–1400.

SAUNDERS, W. B. 1981. A new species of *Nautilus* from Palau. Veliger 24:1–7.

SAUNDERS, W. B. & D. A. WEHMAN. 1977. Shell strength of *Nautilus* as a depth limiting factor. Paleobiology 3:83–89.

STENZEL, H. B. 1964. Living *Nautilus*. Pp. K59–K93. *In:* C. Teichert (ed.), Treatise on invertebrate paleontology, Part K, Mollusca 3. Geol. Soc. Amer. and Univ. Kansas Press.

TUCKER, J. R. & R. H. MAPES. 1978. Possible predation on *Nautilus pompilius*. Veliger 21:95–98.

WARD, P. & M. K. WICKSTEN. 1980. Food sources and feeding behavior of *Nautilus macromphalus*. Veliger 23:119–123.

WODINSKY, J. 1969. Penetration of the shell and feeding on gastropods by *Octopus*. Amer. Zool. 9:997–1010.